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den påverkas av tredimensionell
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Examensarbete i ämnet biologi

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Umeå

2017

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Credits: 30 HEC

Level: A2E

Course title: Master degree thesis in Biology at the Department of Wildlife, Fish, and Environmental Studies

Course code: EX0764

Programme/education:

Place of publication: Umeå

Year of publication: 2017

Cover picture:

Title of series: Examensarbete i ämnet biologi

Number of part of series: 2017:14

Online publication: <http://stud.epsilon.slu.se>

Keywords: Birds, species richness, vegetation structure, Lidar, laser data, bird point census count, Bird National Monitoring Program

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Abstract

Bird populations across the world are in danger with decreasing numbers and more species continually becoming red-listed. One main driver behind this trend is human-caused habitat loss and degeneration, which in particular has been identified as a major threat in forested regions. The importance of forest vegetation structure for bird diversity has been shown in many studies, though typically for small restricted study areas. Here I used a large region of interior boreal Sweden as study area. I used point census count data from the Swedish National Bird Monitoring program combined with recently published nation-covering lidar data, to investigate how bird species richness was affected by 3D forest structure. In total 37 forest-associated bird species were included. Non-parametric random forest models and generalized linear models (GLMs) were used, rendering R^2 values of 36% and 15%, respectively. Variation in vegetation density and canopy height were the two most important forest structure features to predict bird species richness. Height evenness, also known as foliage height diversity (FHD), scored low in variable importance despite being considered a significant driver of bird diversity by many authors. A constrained correspondence analysis (CCA) ordination method was performed to explore habitat selection and niche width for individual bird species. Species with similar habitat preferences were nested in the CCA diagram but showed large overlaps, suggesting that there is a signal in the data but also much noise. Thus, separating between habitat generalists and specialists was not possible. For conservation applications and prioritizations, bird species richness is not necessarily a suitable measure. Rather, the contribution to beta and gamma diversity, as well as the specific habitat preferences of rare, red-listed and specialist species, should guide conservation measures and forest management practices. Future studies should extend further towards a landscape-based study design where forest fragmentation and configuration are significant components.

Introduction

Human-induced habitat change is estimated to have caused global bird population to decrease by 25 billion individuals, equal to 20%, from pre-agricultural times until 1990 (Gaston et al 2003). Globally, 85% of the threatened bird species are at risk mainly due to habitat loss and degradation (Birdlife International 2000). Habitat loss is one of the greatest threats worldwide, not only to birds but to overall biodiversity (Sala et al 2000, Hansen et al 2001, Travis 2003, Canziani et al 2007, Rands et al 2010, Pereira et al 2010). This threat is particularly evident in forested regions (Turner 1996, Siitonen 2001, Fahrig 2003, Nordlind and Östlund 2003) as a large proportion of the world's forests have been extensively modified by human land use (Houghton 1994). Swedish forests are no exception (Nordlind and Östlund 2003) with the majority of productive forests managed for timber production since a long time (Fries et al 1997, Lindahl et al 2015). Clear-cutting, where mature trees are cut and replaced by an even-aged generation of planted saplings, is the prevailing form of forest practice. Planted even-aged forests have different structures than primary forests, both vertically and horizontally (Shorohova et al 2009).

Forest structure influence biodiversity of various taxonomic groups such as fungi (Siltonen 2001), arthropods (Halaj et al 2000, Tanabe et al 2001) and mammals (Carey and Wilson 2001, Williams et al 2002). For birds, the relationships between forest structure, bird abundance and species composition have been explored in many studies. MacArthur and MacArthur (1961) measured the proportion of leaves in different height intervals of the

forest. This evenness of leaf distribution, termed foliage height diversity (FHD), was shown to have a positive correlation with bird species diversity. DeGraaf et al (1998) surveyed forest bird species in managed forests in New England and found significant correlations between forest stand structure and bird abundance for 30 of the 31 species studied. James and Wamer (1982) used bird census data from various forests throughout the United States. The number of bird species showed a strong positive correlation with canopy cover and the number of tree species. Their analyses also emphasized the importance of deciduous trees for bird abundance.

Niche theory

Higher bird species richness in more structurally complex forests relates to a keystone concept of ecology – the niche theory. The term was coined in the 1910s but became popularized in the 1950s by Hutchinson (1957, 1959). According to the theory, each species has specific requirements of resources such as food, habitat, nest sites, light and nutrients. This set of requirements characterize the species' "niche" within which it is able to live and reproduce. The niche span is wide for generalist species and narrow for specialists. For species to co-exist in the same habitat, some degree of niche separation is generally needed (Svärdson 1949). Classic examples are habitat use of the closely related Galápagos finches (Grant 1986) and the separation of foraging behavior in mixed winter flocks of tits (Paridae) and the Goldcrest (Alatalo et al 1987). Cody (1978) studied Sylviidae warblers in England and Sweden and found some degree of niche separation between species. Anderson and Shugart (1974) found differences in habitat preferences within the bird families Picidae, Parulidae, Paridae and Thraupidae. Such habitat partitioning could be a strategy to reduce competition between closely related species. Structurally complex forests are able to provide a greater variety of microhabitats and microclimates which can produce more diverse food sources and potential nest sites (Whittaker et al 2001, Hill et al 2004) and thus harbor more species.

Lidar

For a long time, research studies on how bird species richness and community composition relate to forest structures were performed using field measurements of structural attributes. The emergence of lidar (light detection and ranging) allowed production of high-resolution continuous data on forest structure for large areas and not only for specific points or small sample plots (Bergen et al 2009). Raw lidar measurements can easily be summarized at various spatial scales which is an advantage that has been exploited in some studies (Seavy et al 2009). The vertical dimension gives lidar a large advantage over other remote sensing techniques, especially for studies of forests where the vertical dimension is pronounced. Satellite and aerial imagery cannot fully represent the 3D structure of forests (Miller 1996, Lefsky et al 2002). Additionally, lidar data are continuous which may better represent forest variation than discrete classes (Brown 1998). For a review of lidar and its application in ecology, habitat suitability and biodiversity modeling, refer to Vierling et al (2008) and Bergen et al (2009).

Lidar has successfully been used to model overall bird species richness (Goetz et al 2007, Huang et al 2014, Lindberg et al 2015) as well as to assess habitat suitability for individual species (Hill et al 2004, Graf et al 2009, Seavy et al 2009, Goetz et al 2010). Most studies, however, have been restricted to small study areas (but see Huang et al 2014). Thus, the emergence of large-scale lidar scans enables such studies for whole landscapes and

biogeographical regions. In this study, I used data from the Swedish national lidar scan project (Lantmäteriet 2016) for a large landscape of interior Sweden. Forest structure metrics derived from the raw lidar data were coupled with bird point census count data, 1996-2016, from the National Bird Monitoring Program (Green et al 2016).

Aim / Hypothesis

With reference to the niche theory and habitat partitioning between species, I hypothesize that structurally complex forests have higher species richness than structurally poor forests. Specifically, I ask the following questions:

- What forest structures are the most important for bird species richness?
- What species are generalists and specialists in their habitat choice?

Material and methods

Study area

The study area consists of the interior parts of central Sweden stretching from northern Värmland through Dalarna, Gävleborg, Jämtland and Västernorrland counties (fig. 1). It covers 80 000 km². The study area was selected to correspond to strata 8 in the NILS landscape biodiversity monitoring system (National Inventory of Landscapes in Sweden; Ståhl et al 2011), basically representing the southern part of the boreal interior of northern Sweden. The climate varies slightly within the study area with a mean annual temperature (2007-2016) of 4.5°C in the south and 2.7°C in the north (Swedish Meteorological and Hydrological Institute 2017). There is also a trend of lower temperatures and higher precipitation in the western parts compared to the eastern.

Forested land (as classified by Svenskt Marktäckedata 2000) accounts for 65% of the area. Most forests are managed and only 0.9% of the study area, including forests, lakes, wetlands etc., is protected as nature reserves or national parks (Swedish Environmental Protection Agency 2017).

Bird data

Bird data were retrieved from the Swedish National Bird Monitoring Program which was started in 1996. Monitoring routes are systematically placed in the landscape in a grid, 25 km apart. Each route is 2km x 2km with 8 survey points (fig. 2). The point in the southwest corner (p1) is by design surveyed first, and p8 last. The survey is performed during morning hours (4-10 am) under favorable weather conditions primarily in June, by competent volunteers as well as professionals.

The point-counts are 5-min long with unlimited radius. All birds seen or heard are registered. The survey points are ideally revisited yearly, though most are revisited every second or third year and some points less regularly. This monitoring design also includes linear transects connecting the points. However, transect data were not included in this study.

Bird species selection

All bird species are registered in the bird monitoring program, however, not all species were of interest in this study. Only forest-associated species were included, a total of 37 species listed in Appendix 1. The following categories of bird species were excluded:

Non-forest species. This includes both true open-land species such as the Skylark (*Alauda arvensis*) and the Curlew (*Numenius arquata*), wetland-species such as ducks and shorebirds, as well as species commonly found in edge-habitats and in close proximity to humans, such as Yellowhammer (*Emberiza citrinella*), Fieldfare (*Turdus pilaris*) and Magpie (*Pica pica*).

Species that move across large distances during the time period when monitoring is performed. This includes species with large territories and feeding areas such as birds of prey and most corvids, as well as species that breed early in the season like the crossbills (*Loxia sp.*) and the Eurasian siskin (*Spinus spinus*). Because they move over such large areas they are not closely linked to a specific forest patch and the vegetation structure of that patch.

Sample plots

The bird monitoring sample plot is a circle with the survey point at its center with an unlimited-radius design. To determine the radius of the sample plot I estimated bird detection distance. A too small radius would increase the risk of “false presences”; birds that were detected outside the sample plot. A too large radius would increase the risk of “false absences”; birds that were indeed inside the sample plot but too far away to be aurally identified.

Allredge et al (2007) quantified detectability of singing passerines from various distances. Up to 100 m distance detectability was close to 100%, but beyond that it dropped drastically. Simons et al (2007) found that the maximum average detection distance for two singing passerine species varied between 114 and 157 m. However, this was under experimental, ideal conditions, and when testing in breezy conditions with more birds singing and background noise, Allredge et al (2007) found that the detectability decreased substantially.

Based on the above studies, I chose a 100m radius on my sample plots. Each sample plot thus has an area of 3.14 ha. All sample plots not completely within land classified as forest (National Land Cover Data, Svenskt marktäckedata, 2000) were excluded from the analysis.

Only sample plots surveyed at least five times were included. This limit was used to further reduce the risk of false absences as weather, variation in song activity and chance will influence detectability for sample plots visited only once or a few times.

A total of 224 sample plots were used in the analyses. It should be noted that presence data were handled indifferently regardless of how many years a specific species had been observed within a sample plot.

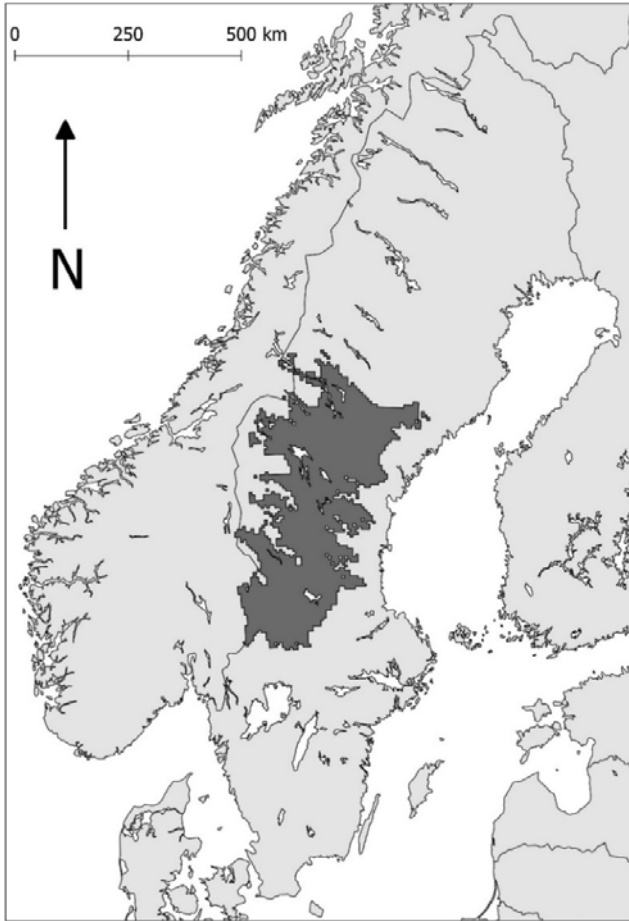


Figure 1. Study area (dark grey), corresponding to strata 8 in the NILS landscape biodiversity monitoring system. Background maps are open source from Natural Earth, [naturalearthdata.com](https://www.naturalearthdata.com).

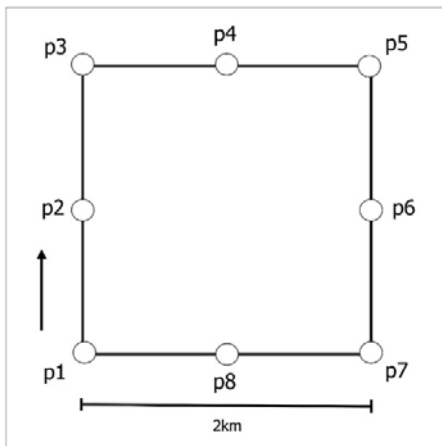


Figure 2. Design of the bird monitoring program. Start is typically at p1 at 4.00 am and p8 is visited around 9 am.

Lidar data

A nation-wide project to laser-scan the whole of Sweden started in 2009 and by the end of 2015, 97.5% of the productive forest land had been scanned. The scanning was done from a small airplane flying 1700-2300 m above ground emitting laser pulses towards the surface with a density of 0.5-1 pulses/m². Leica, Optech, Riegl and Trimble scanners were used. They use slightly different methods for retrieving and storing lidar data, but the data can be treated equally for most applications (Lantmäteriet 2016). A majority of the study area (79%) was scanned leaf-on while a small portion was scanned leaf-off. The fact that a forest is scanned leaf-on or leaf-off can produce significantly different results and therefore sample plots scanned leaf-off were omitted from the analysis. For a more detailed information about raw laser data and the methods used to obtain it, refer to Nilsson et al 2015. Survey plots located in forests that were logged after the scan were identified using data from the Swedish Forestry Agency (2017) and those survey plots were omitted from the analysis.

From the raw laser data, 19 forest structure metrics were produced using the Gridmetrics program in the software Fusion/LDV (McGaughey 2015). Each metric was calculated for 12.5m x 12.5m grid cells and exported as ASCII files which were converted to raster files in Arcmap (version 10.3), resampled to 2.5 x 2.5 m grid cells and then clipped to the sample plot polygons. The grid values were then averaged within each sample plot.

The final lidar dataset consisted of one response variable (species richness) and 19 predictor variables (forest structure metrics).

Forest structure metrics

All forest structure metrics used are listed in table 1. For all metrics, except *height evenness*, both mean and standard deviation were calculated and used as separate predictors. The metrics *0-2m*, *2-5m*, *5-10m*, *10-15m*, *15-20m* and *20-25m* are all tree height intervals and denotes the proportion of laser pulse returns within each interval. The *p95* metric is the 95th percentile height for all returns above the height cutoff 1.5 m, thus *P95* is an estimate of canopy height. The *1st above 1.5m* is the proportion of first returns above 1.5 meters ($1^{\text{st}} \text{ returns} > 1.5\text{m} / \text{all } 1^{\text{st}} \text{ returns} \times 100$). It is a measure of the density of the forest and higher values indicate denser forest.

Canopy relief ratio (CRR) is calculated as: $\text{Canopy relief ratio} = \frac{H_{\text{mean}} - H_{\text{min}}}{H_{\text{max}} - H_{\text{min}}}$. All returns are used. CRR measures the proportion of vegetation located in or close to the canopy, with high values indicating that the vegetation is clustered towards the top of the canopy.

Height evenness is a measure of how evenly distributed, in vertical terms, the vegetation is. Higher values indicate more evenly distributed vegetation whereas low values indicate that most vegetation is limited to a certain height interval. A similar metric, called *foliage height diversity* (FHD) has been suggested to be important for bird species diversity (MacArthur and MacArthur 1961, but see James and Wamer 1982). *Height evenness* was derived from the height interval metrics using this formula:

$$\text{Height evenness} = - \frac{(\ln HI_1^{HI_1} + \ln HI_2^{HI_2} + \ln HI_3^{HI_3} + \ln HI_4^{HI_4} + \ln HI_5^{HI_5} + \ln HI_6^{HI_6})}{\ln 6}$$

This is the formula widely used for species evenness, proposed by Pielou (1966) and here applied to proportions between height intervals. The values of HI_i represent the height

intervals 0-2m (*mean*), 2-5m (*mean*) etc. “Ln 6” is used as the denominator because there are six height interval classes. Higher values indicate more evenness between height intervals. The standard deviation of each metric provides a measure of the variation within each sample plot. Some of the metrics are highly correlated.

Statistics

Random forest

I used a non-parametric random forest model (Breiman 2001) including all predictor variables. Random forest models can handle a large number of input variables without overfitting (Breiman 2001, Biau 2012). This method also handles correlated variables well which eliminates the need for any *a prio* variable selection, which makes the model a particularly suitable choice for this study.

Random forest (e.g. Genauer et al 2008) is a decision tree machine learning technique which is based on a large number of individual decision trees. Together the trees make up a forest and the final model is an average of decisions from all trees. Each tree is trained on a random subset of data as well as a random subset of variables, called “training data”. The training data are different for each tree and randomly selected using bootstrapping. With this method, there is no need to set aside a specific portion of the data for cross-validation, which allows full use of the data for model building.

The method was run in R (2016) with commands from the package “party” (Hothorn et al 2006, Strobl et al 2007, Strobl et al 2008). The number of trees were set to 2000 and the number of predictors randomly selected in each subset was set to 6. The model was applied to the test data (out-of-bag data, see below) to make predictions for species richness. Each predicted value is an average of the values produced by the 2000 decision trees.

Variable importance

Variable importance was explored by using a measure of “out of bag mean square error” (OOB MSE). The MSE is calculated for each variable and then compared to the MSE of a corresponding pseudo variable where values have been permuted (randomly shuffled). MSE values for actual and permuted variables are compared and results in a measure called “percent increase of MSE” (%IncMSE):

$$\%IncMSE = \frac{MSE^{permuted} - MSE^{actual}}{MSE^{actual}}$$

Higher %IncMSE values indicate more important variables. In the standard random forest package, computation of variable importance has been showed to be biased towards correlated variables (Strobl et al 2008). To handle this I used a conditional variable importance measurement that better reflects the true variable importance, which is provided by the “party” package in R (Hothorn et al 2006, Strobl et al 2007, Strobl et al 2008).

Table 1. Laser-derived forest structure metrics used in the analysis.

Laser-derived forest structure metrics	
<i>0-2m (mean)</i>	<i>0-2m (sd)</i>
<i>2-5m (mean)</i>	<i>2-5m (sd)</i>
<i>5-10m (mean)</i>	<i>5-10m (sd)</i>
<i>10-15m (mean)</i>	<i>10-15m (sd)</i>
<i>15-20m (mean)</i>	<i>15-20m (sd)</i>
<i>20-25m (mean)</i>	<i>20-25m (sd)</i>
<i>CRR (mean)</i>	<i>CRR (sd)</i>
<i>p95 (mean)</i>	<i>p95 (sd)</i>
<i>1st above 1.5m (mean)</i>	<i>1st above 1.5m (sd)</i>
<i>Height evenness</i>	

Generalized linear models (GLMs)

Additionally, I used an automated generalized linear model (GLM) selection technique where models with all possible combinations of predictors were evaluated. As the number of combinations grows exponentially with the number of predictors, I introduced a limit of maximum 5 predictors in each model to keep computation time reasonable. All possible combinations of models with 1, 2, 3, 4 or 5 predictors were evaluated, resulting in a total of 11 628 models. The models were ranked according to their AICc value. AICc is recommended over AIC as it reduces the risk of overfitting when n is not many times larger than p^2 (n = number of sample plots, p = number of predictors) (Claeskens and Hjort 2008, Giraud 2015). A null model ($y \sim 1$) was run and evaluated in the same way for comparison. The AICc difference between models (Δ_i) can be used to compare models and is calculated like this: $\Delta_i = AICc_i - AICc_{min}$, where $AICc_i$ is the value for the model i , and $AICc_{min}$ the value for the best model. As a rule of thumb, Δ_i values < 2 indicate that the model has substantial support (Burnham and Anderson 2003).

Variable importance

The importance of each predictor was calculated and defined as the sum of Akaike weights over all models that included that predictor. The more high-ranked models a specific predictor appeared in, the higher its importance value. Predictors that mostly appeared in low-ranked models got a low importance value. To perform the analyses I used the “dredge” and “importance” commands from the R package “MuMiN” (Bartón 2016).

Constrained correspondence analysis (CCA)

To understand the habitat selection of individual species I used an ordination method called constrained correspondence analysis (CCA) (ter Braak 1986). CCA can handle data with a lot of noise and correlated environmental variables (Palmer 1993) and is therefore a preferred ordination method for this kind of data. CCA performs weighted linear mapping

based on Chi-squared distances. Basically, the CCA method looks for the linear combinations in environmental variables that are maximally correlated with the linear combinations of presence/absence data of all species included. A two-dimensional ordination diagram is produced from the environmental variables, in this case the predictor variables, and the weighted average for each species is plotted in this diagram (ter Braak 1988). Standard deviation for each weighted average was also calculated and was used to assess variation in habitat selection of individual species and to distinguish between generalist and specialist species. The analysis was performed using the R package “vegan” (Oksanen et al 2017).

Results

Random forest

The random forest model including all predictor variables had an R^2 -value of 35.7%, which indicates that the relationship between species richness and predictors is weak. The predictive performance of the model is visualized as a scatter plot where predicted values are plotted against observed values (fig. 3). Each predicted value is an average of the values produced by 500 decision trees. The 1:1 relationship line is also plotted. Points close to the 1:1 line are better predicted than points far away. Observed species richness span from 5 to 23 species, while the predicted values are concentrated in the range of 10-15 species.

The most important variables were *Ist above 1.5m (sd)* (18.3%), *p95 (mean)* (8.7%) and *CRR (mean)* (6.8%).

Generalized linear models (GLMs)

The three best GLMs according to AICc value are presented in table 2. AICc values for the three best models varied between 1108 and 1109.4, and R^2 values 15.0%-15.5%. All three top models contained the variables *10-15m (sd)*, *2-5m (sd)* and *20-25m (mean)*. The variable *Ist above 1.5m (sd)* was present in two of the top three models. The null model scored an AICc value of 1137.9 and an R^2 value of 0%. The top 18 models scored Δ_i values < 2 , the cut-off value indicating models with substantial support according to Burnham and Anderson (2003).

Variable importance was calculated as the sum of Aikake weights for all models that included each specific variable (fig. 4). Variables that are included in high-ranked models received high variable importance. *Ist above 1.5m (sd)*, *10-15m (sd)* and *20-25m (mean)* were the three most important variables.

Constrained correspondence analysis (CCA)

A constrained correspondence analysis (CCA) was performed and produced a two-dimensional ordination diagram from the environmental variables (predictors) (fig. 5). Weighted averages from presence/absence data were plotted for individual species and generated a diagram where the axes represent the habitat characteristics of the forest and the plotted points the habitat selection of each species. In fig. 6, standard deviation ellipses for individual species were added to show variation in habitat selection. Larger ellipses represent larger variation in habitat selection. As shown in the diagram, ellipses for all species are large with much overlap, and it is not possible to distinguish between generalist and specialist species.

Willow ptarmigan, lesser spotted woodpecker and grey-headed woodpecker were only observed in one single sample plot each, and were therefore not included in this analysis.

Table 2. The three highest ranked GLM models according to the AICc value, and the null model.

Model	Formula	AICc value	R ² value
Model 1	Bird species richness ~ 10-15m (sd)+ 1st above 1.5m (sd) + 2-5m (sd)+ 20-25m (mean) + 1	1108.0	15.3%
Model 2	Bird species richness ~ 0-2m (sd) + 10-15m (sd) + 2-5m (sd) + 20-25m (mean) + 1	1108.8	15.0%
Model 3	Bird species richness ~ p95 (mean) + 10-15m (sd) + 1 st above 1.5m (sd) + 2-5m (sd) + 20-25m (mean) + 1	1109.4	15.5%
Null model	Bird species richness ~ 1	1137.9	0%

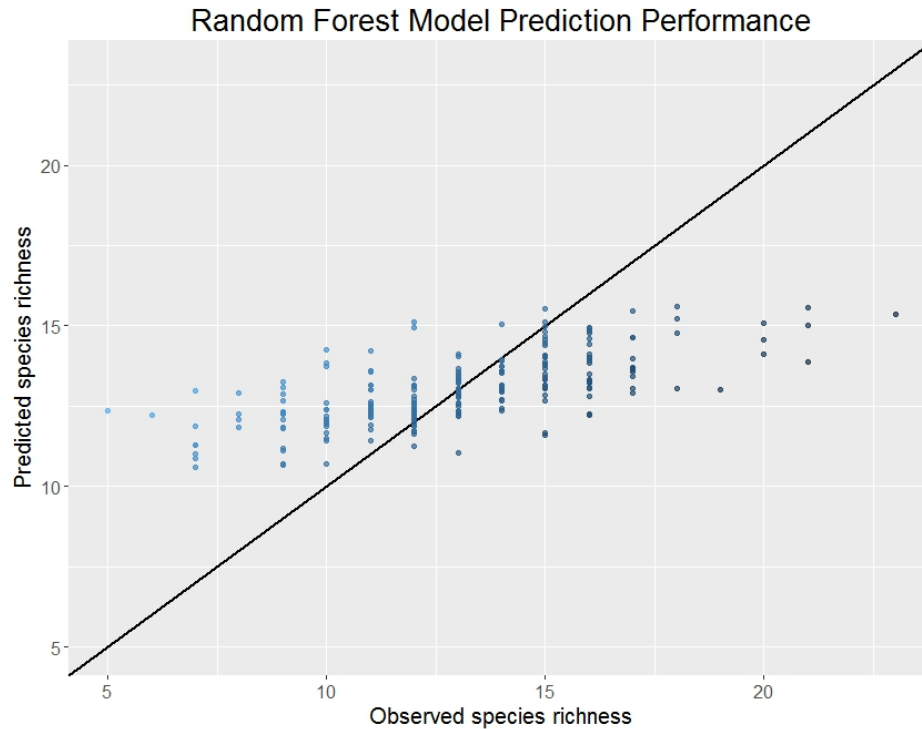


Figure 3. Predicted and observed values of bird species richness from the random forest model. Predicted values are averaged over 2000 individual decision trees.

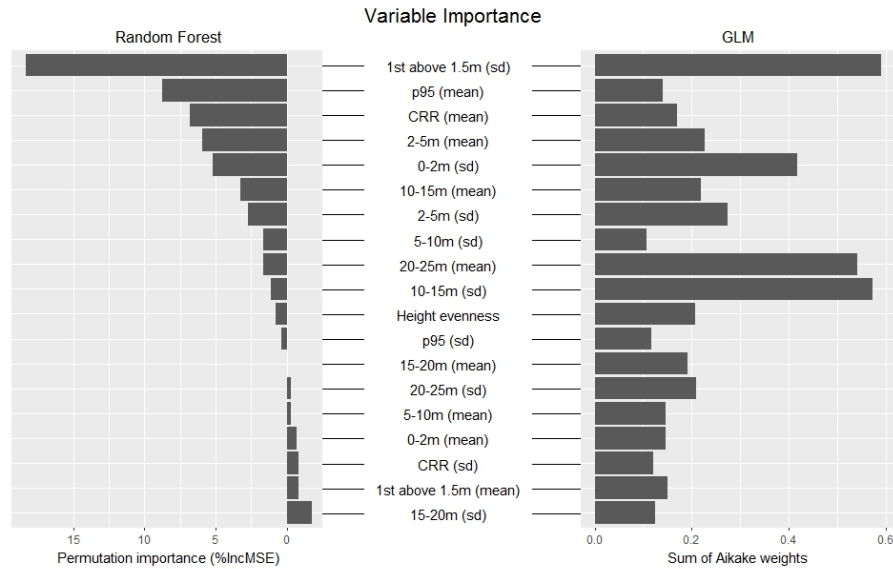


Figure 4. Variable importance for the random forest model and the GLMs, respectively. Variable importance for the random forest model was calculated as $\%IncMSE = \frac{MSE^{permuted} - MSE^{actual}}{MSE^{actual}}$. GLM variable importance is defined as the sum of Aikake weights for all models in which the variable appeared. Higher values indicate higher variable importance.

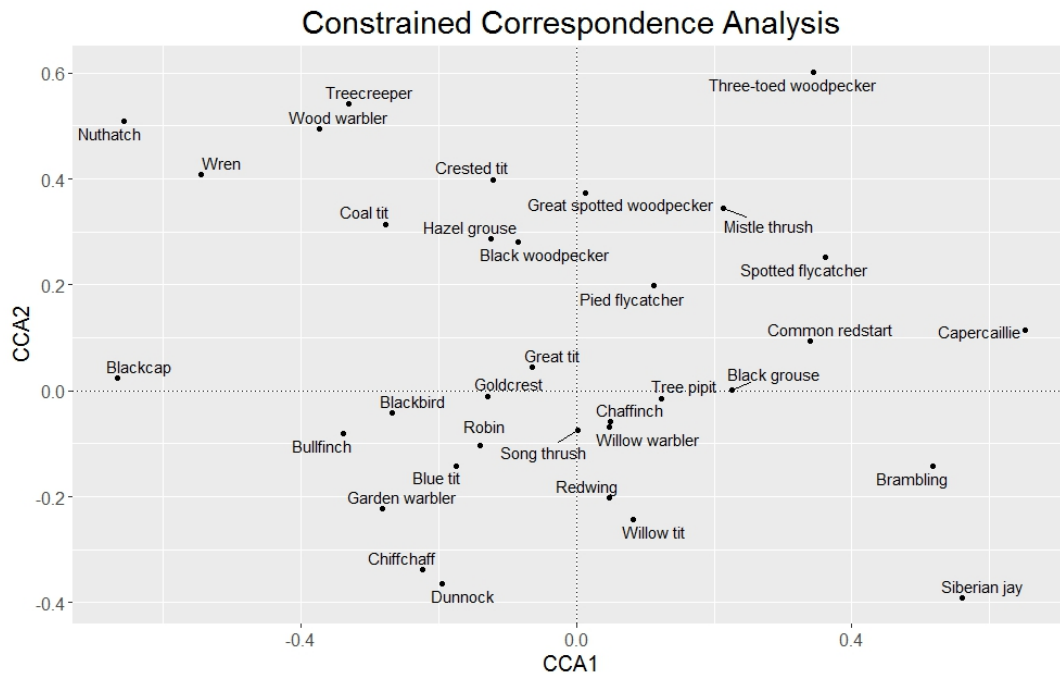


Figure 5. Constrained correspondence analysis diagram. Points represent weighted averages for individual species in a two-dimensional ordination space.

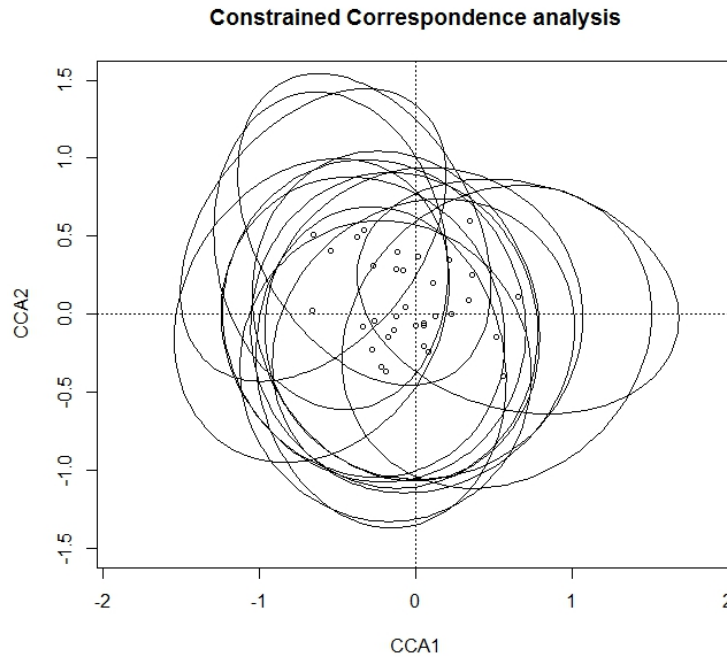


Figure 6. Constrained correspondence analysis ordination diagram. Points represent weighted averages for individual species in a two-dimensional ordination space; ellipses represent the standard deviation for individual species.

Discussion

Study results

The random forest model had an R^2 -value of 35.7 %. While observed values of species richness spanned from 5 to 23 species, most predictive values were within the range of 10-15 species. The three best GLMs scored R^2 -values of 15.0% - 15.3% and AICc values of 1108.0-1109.4, which was significantly better than the null model ($R^2=0\%$, AICc= 1137.9).

The predictor I^{st} above 1.5m (sd) was the most important variable for both random forest and GLM models. This variable should be interpreted as the variation in forest density within the sample plot. It could be described as “patchiness” where high values indicate a forest with both densely and sparsely vegetated patches within the same sample plot. The predictor I^{st} above 1.5m (sd) is strongly correlated with 0-2m (sd), a variable that scored high in the GLM variable importance. The predictor 10-15m (sd) also scored high in GLM variable importance. High values of sd metrics suggest a lot of variation in forest structure, which is important for species richness according to the niche theory.

Forest canopy height, represented in this study by $p95$ (mean) and to some extent 20-25m (mean), was an important predictor of bird species richness. The metric $p95$ (mean) was the second most important variable in random forest whereas 20-25m (mean) was the second most importance variable in GLM. Donald et al (1998) found both species richness and overall bird abundance to increase with forest age. Hinsley et al (2009) concluded tree canopy height to be a strong determinant for bird species assemblages. In the large-scale

study by Huang et al (2014), mean vegetation height was the best metric for predicting richness of interior bird species.

Surprisingly, *height evenness* scored no higher than the average of variable importance and was not included in any of the three top-ranked GLMs. *Height evenness* is a close estimate of the popular *foliage height diversity* (FHD) index (MacArthur and MacArthur 1961). They found FHD to be strongly correlated with *bird species diversity* (BHD). Since then, this concept has been well established and several authors have found similar associations (Karr 1968, Karr and Roth 1971). However, the FHD/BSD correlation has also been subject to a long discussion and does not hold true in all situations. Neither Willson (1974) nor Erdelen (1984) found such correlation when comparing differently structured forest; only when the analysis was extended to include bush habitats could the FHD/BSD relationship be established. Huang et al (2014) found FHD (there referred to as “Shannon’s diversity index”) to be correlated with forest edge bird species richness, but neither to interior nor woodland bird species richness.

Canopy relief ratio (CRR (mean)) was the third most important variable in the random forest model and was positively correlated with bird species richness. The *CRR* metric is a measure of the proportion of vegetation located in or close to the canopy.

The CCA diagram (fig. 5) plots species habitat selection in a two-dimensional space. Interestingly, species with similar habitat preferences (to my experience) appear close to each other in the diagram. E.g., the dunnock and the chaffinch are often found in young- to medium-aged dense spruce plantations, and both species are plotted in the lower left quadrant. There are a handful species that normally are associated with open pine-dominated forests: tree pipit, common redstart, mistle thrush, pied flycatcher, and spotted flycatcher. All those species are plotted in or near the upper right quadrant. The nuthatch, treecreeper and wood warbler are generally found in forests with tall and old trees. The wren, too, selects this habitat as long as there is an abundance of forest floor vegetation and debris (the wren also commonly breeds on clear-cuts, however no sample plots with clear-cuts were included in the analyses). All four species are plotted in the upper left quadrant. The three woodpeckers (great spotted, black and three-toed) are found on the upper half of the diagram. The grey-headed and lesser spotted wood-pecker were excluded from this diagram as each species was observed in only one sample plot, respectively.

From the positioning of species in the diagram, and the knowledge of those species’ habitat preferences, the interpretation is that the x-axis of the diagram represents the density of forest (higher density to the left, lower density to the right) whereas the y-axis represents the height of the forest canopy (tallest trees). If that interpretation is true, the x-axis would be closely associated with the density metric *Ist above 1.5m (mean)*. Since it is obvious that habitat preference for forest density varies across species, it is not hard to understand why *Ist above 1.5m (sd)*, a measure of variation in forest density, was the most important variable in both GLM and random forest models.

In the second CCA diagram (fig. 6) the variation in species habitat selection is plotted as standard deviation ellipses. I expected the size of those ellipses to vary and that large ellipses would indicate generalist species, and small ellipses specialist species. However, all ellipses are large and there is a significant overlap. The interpretation of the overlap is that there is too much noise in the data, too little data, and potentially also that the selected method did not manage to properly distinguish between generalist and specialist species.

Nevertheless, there is a signal in the data at individual species level, as shown in the first CCA diagram.

Methodology

When working with presence/absence data, detectability is an important factor that needs to be taken into account, since several aspects of detectability could potentially bias the results. Habitat structure has been shown to influence detectability by distorting the bird song (Richards 1981) or by affecting the actual song intensity (McShea and Rappole 1997). Bibby and Buckland (1987) compared detection rate in 2-year and 11-year old conifer plantations across species, and found the rate to be four times higher in the 2-year plantations. For the willow warbler (*Phylloscopus trochilus*) the differences were even greater: eight times higher in the 2-year plantations. In general, birds are harder to detect in dense habitats which leads to an underestimation (Buckland 2006) and, consequently, there is a risk that the results in this study underestimated species richness in dense forests and hence resulted in biased values for metrics associated with dense forests.

Detectability also varies across species, e.g. due to different singing intensities (McShea and Rappole 1997, Farnsworth et al 2002), which make comparisons between species precarious, and furthermore that such a comparison may be considered invalid for testing bird density (Buckland 2006). The wood grouse species (capercaillie, black grouse, hazel grouse, willow grouse) are known to have low detectability in May-June; i.e. during the time period when the survey data for this study were collected. Those species are normally detected in the line transects when flushed but rarely observed in the point census counts (Å. Lindström, personal communication, April 25, 2017.). Point data for those species were for that reason excluded in the population estimates presented in Ottosson and Ottvall (2012). To correctly assess presence/absence of wood grouse species, the preferred method is to include all indirect (faeces, traces, feathers) and direct observations (Graf et al 2009). It is difficult to optimally survey all species in multi-species bird monitoring schemes (Buckland 2006).

The amount of monitoring time spent on each point will, obviously, influence detectability (e.g. Diefenbach et al 2007, Leu et al 2017). For the data used here, the point count is standardized to 5 min to account for data bias due to observation duration. However, in this study I used the accumulated number of species over years, and the number of years each plot has been visited varied. To reduce this potential bias I excluded sample plots visited fewer than five times. However, it is difficult to estimate the number of visits needed to detect all species present. As the number of years visited ranged from 5 to 18 years, there could still be some bias not corrected for.

For the woodpecker species, there is a particular risk of false presence. Woodpeckers have loud calls that travel long distances and some of the observations could be from birds sitting outside the 100 meter radius.

Species selection and preferences

According to the niche theory, a more structurally complex forest will provide more niches and therefore harbor more species. However, the theory is not universally true and structurally diverse old-growth forest does not necessarily hold more species, but other species. The different succession stages of a disturbed forest, from clear-cut, to dense even-

aged stands, to mature and increasingly structurally complex forests, i.e. if left unmanaged, will each favor different bird communities. The species turn-over can be dramatic and fast as the forest matures from mid- to late successional stage (Holmes and Sherry 2001). Both species richness (James and Wamer 1982, Morgan and Freedman 1986) and total number of individuals (Holmes and Sherry 2001) can be lower in late- than in mid-successional forests. Less structurally complex forests are typically inhabited by generalist bird species that use a wide range of habitats (Huang et al 2014). Generalist species have broader and more flexible niches, making them more able to co-exist with other species. Specialists, typically interior species dependent on specific forest structures (Hagan et al 1996), are more likely to face greater competition between species which can limit species richness despite high structural complexity (Cody 1974).

In the light of this, one must ask the question: is species richness in individual sample plots the best measure of biodiversity? To answer that question, the rareness of different bird species must be accounted for. Generalist species are often common species and will be found in many different types of forests, woodlands, and even in parks and urban neighborhoods. The great tit and the blackbird are good examples of such species. Because those species are common “everywhere” they do not add much to other measures of biodiversity such as beta and gamma diversity. Anthropogenic large-scale disturbances are major drivers of a process (Devictor et al 2008, Doxa et al 2012) called *biotic homogenization* (McKinney and Lockwood 1999, Olden 2006) where some species (winners) systematically replace other species (losers). Biotic homogenization is a strong and ongoing process in the bird communities of European countries including Sweden (Le Viol et al 2012). Specialist species are found only in specific types of forests with characteristics that are often rare in homogenous landscapes resulting from, e.g., standardized forestry practices. The presence of specialist species in the landscape considerably adds to both beta and gamma diversity.

The study was designed to avoid including birds breeding on clear-cuts, meadows, wetlands and farmlands. Birds breeding in forest edge habitat were excluded to the same extent. To exclude such species and include only true interior species, the buffer zone to any non-forest land class would probably have had to be much larger than 100 m. Thus, it is likely that edge effect was not fully accounted for in this study.

A landscape perspective with emphasis on configuration and fragmentation is necessary to more fully understand the links between forest structure and bird biodiversity. Matlack and Litvaitis (1999) found edge density to be one of the most significant negative factors influencing biodiversity. Forest cover and the configuration of forest patches in the landscape were important predictors of presence of forest-dwelling species in a study performed in eastern Canada (Villard et al 1999). The study area used in this study is highly fragmented by forestry with only 0.9% of the land protected as nature reserve or national park. On a landscape scale, forest “islands”, even though near-natural and structurally complex, in a matrix of monocultures, forest plantations and clear-cuts, are probably not sufficient to harbor interior species.

For reasons discussed above, species richness *per se* is not necessarily a good base for conservation prioritizations. As stated, common generalist species will prevail in managed forest landscapes without conservation measures. Rather, for diversity assessments, focus should be placed on area-sensitive and rare forest species (Robbins et al 1989). Species with specific requirements on their habitat (specialists) are more vulnerable to habitat

variations and will be the first to disappear when there is a change (Brown and Lomolino 1998, Díaz et al 2006).

It should be noted that although species habitat selection has been analyzed in this study, little regard has been paid to *habitat quality*. The bird data used consists of presence/absence data from sample plots, and no consideration has been made to the number of individuals. The assumption is that the more individuals of a certain species, the closer the habitat is to that species' optimal habitat preference. However, assessing habitat quality is not straight-forward because the number of individuals (territories) is also affected by other factors, such as competition (e.g. Svärdsön 1949).

Limitations and prospects

Using data from the Swedish National Bird Monitoring program (Green et al 2016) allowed a large-scale study design. The monitoring practices reduced the bias of false absence. However, the way the data are collected is not designed specifically for the hypothesis tested here. A better-matching monitoring design should have been set up slightly differently: all sample plots should have been visited the same number of times to eliminate any potential bias; a fixed radius point-count is preferred over an unlimited radius; and the sample plots should have been distributed equally between “production forests” and “natural forests”. Lindberg et al (2015) conducted such a study in two small areas in northern Sweden. All sample plots were visited six times in one season and surveyed with 7.5 min fixed radius point-counts. The estimated number of breeding pairs was used rather than presence/absence data.

Culbert et al (2013) and Huang et al (2014) used large datasets from national monitoring programs. In contrast to my study, their analyses were conducted outside the sample plot limitation and applied a wider landscape perspective. For Sweden, a new landscape-covering dataset on potential continuity forests (forests that have not been clear-cut during the past 60-70 years) has just been released (Ahlkrona et al 2016). Using such land-cover data to complement lidar data would be better suited to predict species with larger territories and home-range areas, such as woodpeckers, grouses, corvids and birds of prey.

Conclusions

Two well-defined forest characteristics stand out as the most important for predicting bird species richness: mean canopy height and tree density variation. As interpreted in the analysis, the CCA diagram is oriented according to those two axes. The diagram helps to visualize the difference in habitat preference between species and shows why forest density variation is important. Species that have similar habitat preferences were plotted near each other in the CCA diagram, but with large within-species variation. This suggests there is a signal in the data, but also that the data contain much noise; something that at least partly can explain the relatively low R^2 values produced by the predictive models. Some modifications in the study design would potentially have increased model prediction performance: limit-radius point census counts, a defined number of visits, and a stratified number of samples from different classes of forest complexity. To truly explore the relationships between forest structure and bird communities on a large scale, however, one would need to move beyond the sample plot design and work with fragmentation and

configuration analyses in whole landscapes. Recently published open-source forest data, based on lidar-derived metrics, now allow for such analyses in northern boreal Sweden (Nilsson et al 2015). For conservation applications, a straight species richness measure is not recommended as base for such prioritizations. Rather, the contribution to beta and gamma diversity, as well as the specific habitat preferences of rare, red-listed and specialist species, should guide conservation measures and forest management practices.

Acknowledgements

I would like to thank my supervisor Johan Svensson and my co-supervisors Eva Lindberg, Heather Reese and Karin Nordkvist for the support. I would also like to thank Åke Lindström and Martin Green at Lund University for providing data from the Swedish National Bird Monitoring Program.

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Appendix

Appendix 1. List of bird species included in the analyses and the number of sample plots in which they were observed (N) from the total 224.

Species name	Scientific name	N	Species name	Scientific name	N
Black grouse	<i>Lyrurus tetrix</i>	67	Hazel grouse	<i>Tetrastes bonasia</i>	8
Black woodpecker	<i>Dryocopus martius</i>	57	Lesser spotted woodpecker	<i>Dendrocopos minor</i>	1
Blackbird	<i>Turdus merula</i>	126	Mistle thrush	<i>Turdus viscivorus</i>	99
Blackcap	<i>Sylvia atricapilla</i>	27	Nuthatch	<i>Sitta europaea</i>	6
Blue tit	<i>Cyanistes caeruleus</i>	9	Pied flycatcher	<i>Ficedula hypoleuca</i>	76
Brambling	<i>Fringilla montifringilla</i>	98	Redwing	<i>Turdus iliacus</i>	156
Bullfinch	<i>Pyrrhula pyrrhula</i>	49	Robin	<i>Erithacus rubecula</i>	192
Capercaillie	<i>Tetrao urogallus</i>	10	Siberian jay	<i>Perisoreus infaustus</i>	12
Chaffinch	<i>Fringilla coelebs</i>	224	Song thrush	<i>Turdus philomelos</i>	211
Chiffchaff	<i>Phylloscopus collybita</i>	79	Spotted flycatcher	<i>Muscicapa striata</i>	81
Coal tit	<i>Parus ater</i>	33	Three-toed woodpecker	<i>Picoides tridactylus</i>	8
Common redstart	<i>Phoenicurus phoenicurus</i>	132	Tree pipit	<i>Anthus trivialis</i>	194
Crested tit	<i>Lophophanes cristatus</i>	52	Treecreeper	<i>Certhia familiaris</i>	23
Dunnock	<i>Prunella modularis</i>	98	Willow ptarmigan	<i>Lagopus lagopus</i>	1
Garden warbler	<i>Sylvia borin</i>	51	Willow tit	<i>Poecile montanus</i>	86
Goldcrest	<i>Regulus regulus</i>	147	Willow warbler	<i>Phylloscopus trochilus</i>	221
Great spotted woodpecker	<i>Dendrocopos major</i>	81	Wood warbler	<i>Phylloscopus sibilatrix</i>	18
Great tit	<i>Parus major</i>	127	Wren	<i>Troglodytes troglodytes</i>	60
Grey-headed woodpecker	<i>Picus canus</i>	1			

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